STUDIES ON THE INHERITANCE OF GLUME COLOUR AND REACTION TO STEM RUST AND SMUT IN OATS

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By John Nicholas Welsh.

Introduction.

Oats, which are grown the world over as a food for man and domesticated livestock are of considerable importance in Canada, being exceeded in value only by wheat. The total yield and value of the crop are limited by a number of factors such as soil, moisture, temperature and diseases. Among the most destructive agents are the disease producing fungi, rust and smut.

These diseases may be controlled either by the application of chemical substances to the seed or to the growing plant. Since chemical treatments involve expense and are not always successful, the production of resistant varieties appears to be the most economical and effective means of controlling plant diseases. Already much has been accomplished in the production of resistant varieties and in the study of the inheritance of resistance to certain diseases. However, owing to the existence of physiologic specialization in a number of disease producing fungi, the production of resistant varieties has become a complicated process. A fact of great importance to one who seeks to improve plants by breeding for disease resistance, is that this character obeys the same fundamental laws of inheritance as plant characters in general.

The object of the investigations herein reported is to study the mode of inheritance of various plant characters and

to produce high yielding strains of oats resistant to stem rust and smut. Seven physiologic forms of oat stem rust, Puccinia graminis avenae (Pers.) Erikss. and Henn., have been identified in Canada. The ultimate aim is to study the inheritance of the mode of reaction to each of these forms and to combine the resistance to all of them in a single variety. Although there is evidence of physiologic specialization within the loose and covered smuts of oats, Ustilago avenae (Pers.) Jens. and Ustilago levis (K. and S.) Magn. respectively, little definite information is available regarding the number of forms. Therefore, until further research reveals the necessary information, the process of synthetically building up resistance to specific smut forms is not possible. The production of desirable varieties resistant to smut need not be delayed, however, as certain varieties are known to be resistant when inoculated with composite cultures of the pathogene collected at random in the field.

Literature Review.

Rust Reaction.

Among the earliest observations on the variation in susceptibility of varieties to rust are those of Eriksson and Henning (8) in Sweden. These writers state that it was impossible to observe any definite difference in the susceptibility of oat varieties. McAlpine (23) states that stem

rust alone is peculiar to oats in Australia and that the wild oat, Avena fatua, is generally severely affected. Vavilov (47) made extensive tests on 350 lots of cultivated and wild oats to determine their reaction to both stem and crown rust. From his experiments he concluded that there is little probability of finding varieties resistant to stem rust. In the case of crown rust, however, although the majority of cultivated and wild oats were found to be very susceptible, many more forms showed resistance. One of the earliest American records of rust resistance in oats was that of Speers (42) in 1870, who reported the results of his observations on the occurrence of rust on the oat varieties in the Iowa Agricultural Experiment Station plots. Though no mention is made of the species of rust concerned, he states that the oats all rusted so badly that they were almost worthless, with the exception of Improved American, Everett, Lackawana and Giant Yellow French. Other early writers who observed resistance or susceptibility of oat varieties to rust are Pammel (29), Plumb (32), Carleton (5), Bolley (3), Shepperd and Ten Eyck (41) and McWethy (25).

Norton (27) published definite experimental results on oat rust resistance and distinguished clearly between crown rust, Puccinia coronata avenae (Corda.) Erikss. and Henn., and stem rust, Puccinia graminis avenae. He found that Avena sterilis forms were comparatively free from crown rust but susceptible to stem rust.

Parker (30) studied the resistance of oat varieties to crown and stem rust under greenhouse conditions, using seedlings and mature plants. Of more than 120 strains tested 80 were found to be entirely susceptible to both rusts at both stages of growth. Only two varieties, White Tartarian and Ruakura Rustproof were found to be resistant to stem rust.

In a later work, Parker (31) studied the resistance of two oat varieties, Burt and Sixty Day, to both stem and crown rust, together with F_2 hybrids between these two varieties. Most of the inoculations were made on seedlings, but enough were made on plants at the time of heading to show that the results were similar. As both parents were susceptible to stem rust, no resistant segregates were obtained in the F_2 generation.

Durrell and Parker (7) made a comprehensive study of varietal resistance to both crown and stem rusts, both in the field and in the greenhouse. Although the manifestations of resistance to rust in the field and greenhouse were comparable, it was, however, more marked in the field. The results of the varietal experiments conducted in the greenhouse indicate that the varieties of the red oat group, Avena sterilis, show more resistance to crown rust than those of the common oat group, Avena sativa. The most resistant varieties in the species of Avena sterilis were found to be Appler and Red Rustproof. The varieties White Russian and Green Russian of the Avena sativa group and

Parker (10) studied the resistance of oat varieties to crown and stem rust under greenhouse conditions, using rec lings and mature plants. Of more than 180 stocking tested were found to be entirely susceptible to both rusts at bo stages of growth. Only two varieties, White Tartarian and Markton Westproof were found to be resistant to stem rust.

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the strains grown under the names Avena sativa grisea and Avena orientalis mutica were resistant to stem rust, while the variety Ruakura and Avena barbata were resistant to both rusts.

There are apparently more varieties of oats which show resistance to crown rust than to stem rust. Under rust nursery conditions the varieties White Russian, Green Russian, Ruakura and the species Avena barbata, Avena orientalis mutica and Avena sativa grisea showed a high degree of resistance. The species Avena barbata and the varieties Green Russian and Ruakura were the only oats showing marked resistance to both smuts under the conditions of the experiment.

Mackie and Allen (22) made a study of the resistance of oat varieties to stem rust. These writers inoculated 217 varieties of oats and the following were found to be resistant: Richland, Ruakura, Snoma, one lot of Green Russian and all lots of White Tartar.

Levine (20) made an extensive study during the period 1923-1927 of varietal resistance to stem rust of oats. The following eight varieties, selections and crosses were most resistant during the period under review: Iogold, Hajira, Richland, Minota x White Tartar (White Russian), White Tartar, Green Mountain, Anthony and Edkin.

A study of the inheritance of resistance to stem rust was first made by Garber (12) in 1921. This writer made

both roots.

crosses between White Russian, a resistant variety, and two susceptible varieties, Minota and Victory. There was evidence of a single factor difference between the parents in both crosses and resistance appeared to be dominant.

Garber (13) made a more complete study of the above crosses in the F_1, F_2 and F_3 generations. The F_1 plants were resistant and in the F_2 a ratio of 3 resistant plants to 1 susceptible was obtained. The breeding behavior of the third generation substantiated the results obtained in the second. Resistance in these crosses was found to be dominant and governed by a single factor. Griffee, 1922 (17), obtained similar results.

Stakman, Levine and Bailey (43) first investigated the possibility of physiologic specialization in the stem rust of oats, Puccinia graminis avenae. From their investigations they concluded that four biologic forms existed and were apparently constant. Furthermore, these writers concluded that physiologic specialization may be different in different countries, and also may differ even in various regions of the same country. On the other hand, more than one biologic form may occur in the same locality or even on the same plant.

Bailey (1) proved definitely that five physiologic forms existed in the United States. Gordon and Bailey (16) showed that seven physiologic forms occur in Canada.

Hayes et al (18) studied the inheritance of resistance in three crosses and obtained a segregation in F_2 of 3 resistant

plants to 1 susceptible. Resistance was found to be dominant.

Dietz (6) likewise found resistance to be dominant and due to a single factor difference in crosses between White Tartar x National and White Tartar x Lincoln. In crosses between resistant varieties the F_1 plants were resistant. In the F_2 generation some plants were produced which were more resistant than either parent.

The same writer crossed three susceptible and genetically different strains of the Burt oat with White Russian, and obtained varying results. In one cross the F_1 was susceptible and the F_2 segregated in the ratio of 3 resistant to 13 susceptible plants. In another cross the F_1 was resistant and the F_2 segregated in the proportion of 3 resistant plants to 1 susceptible. In still another cross the F_1 was susceptible and the F_2 segregated in the ratio of 1 resistant to 3 susceptible plants.

With the exception of Dietz, in his study with the three different strains of Burt, all investigators have agreed regarding the inheritance of rust resistance. Although physiologic specialization exists within Puccinia graminis avenae, a fact which complicates the study of rust resistance and the production of rust resistant varieties, no one as yet has attempted to study the inheritance of separate physiologic forms, or endeavored to combine resistance to all forms.

Smut Reaction.

Previous to the work of Reed (33) in 1920, very little study had been made of the resistance of oat varieties to loose smut, Ustilago avenae, and covered smut, Ustilago levis. This author gives a complete review of the literature regarding early studies on smut resistance, so in the present review the more recent work, only, shall be reported.

McAlpine (24) successfully infected both wild and cultivated oats with spores of Ustilago avenae from wild oats. He also infected wild oats with spores from cultivated oats.

Heald (19) reported results with 19 varieties of oats inoculated with spores of Ustilago levis. Three varieties of hulless oats (Avena nuda) had more than 87 percent infection. Infections ranging from 27.5 to 73.2 percent were shown on 14 varieties, mainly Avena sativa types. Two varieties showed negative results. One of these, Texas Red, belonged to the Avena sterilis group and the other, Kherson, belonged to the Avena sativa group.

Vavilov (46) reported his observations on the behaviour of a large number of varieties of oats infected with Ustilago avena. The only immune variety of Avena sativa obtained by this writer was Mesdag. Under field experiments this variety was found to be free from smut, but under greenhouse conditions he was able to obtain an occasional smutted plant. Vavilov also records resistance to loose smut

in Avena nuda var. biaristata. This variety, unlike other varieties of Avena nuda has 14 to 16 chromosomes. He also records one strain of Avena strigosa which proved to be susceptible to loose smut.

Reed (33) obtained results which coincided very closely with those of Vavilov. The only immune variety, Mesdag, observed by Vavilov appeared to be identical with the variety Black Mesdag used by Reed.

Reed described his experiments on the resistance and susceptibility of species and varieties of Avena to both loose and covered smuts. It was found that all the strains of the species Avena brevis Roth. and Avena strigosa Schreb. were entirely free from infection. Avena fatua L. proved quite susceptible to both smuts, as likewise did the strains of Avena nuda L. All the varieties and strains of Avena sativa orientalis were moderately susceptible, the infection averaging above 50 percent. The large number of strains and varieties of Avena sativa L. showed a considerable range in the degree of susceptibility to both smuts. A few varieties proved very susceptible, but the majority showed only moderate percentages of infection. Two strains of Black Mesdag consistently showed negative results.

It is especially noteworthy that the highly susceptible varieties were equally susceptible to both smuts, the highly resistant varieties were equally resistant to both smuts, and varieties that consistently showed negative results with one smut behaved similarly towards the other.

Stapledon (44) has noted the prevalence of smut in the varieties of oats at the Welsh Plant Breeding Station at Aberystwyth. His results are more significant on the question of contamination of seed than on the problem of varietal resistance. It should be noted, however, that Welsh strigosa, belonging to the Avena strigosa group, produced some smutted plants.

Sampson and Davies (40) have recorded the occurrence of Ustilago avenae on 31 varieties in the experimental plots at Aberystwyth, Wales. Fifteen of these, among them the varieties Culberson, Black Mesdag, Golden Rain and Black Mogul, appeared to be quite susceptible. According to these investigators, Ustilago levis is rare in Wales, having been found in the experimental plots only on Avena nuda var. chinensis and Avena strigosa sub-species glabrescens and orcadensis. They carried out an experiment in which they inoculated eight varieties of oats with spores of Ustilago levis from Orkney strigosa.

Infections were obtained on Orkney strigosa, but the other seven varieties, Algerian sterilis, Welsh strigosa, Ceirch au Bach, Black Tartar, Golden Rain, Rodnorshire, Sprig and Potato gave negative results. According to their other records, however, these varieties were severely infected by Ustilago levis.

The results obtained by these investigators differ from those of Reed (33) in that Black Mesdag and different

varieties of Avena strigosa were susceptible. Reed obtained varieties of Avena strigosa from the Welsh plant breeding station and found that they differed in appearance from the ones with which he worked.

Reed (35) in a later work, made a comprehensive study of the varietal resistance of oats to Ustilago avenae and Ustilago levis. Avena sativa was represented by over 90 varieties and 182 strains. These showed great variation in their susceptibility. A few proved to be very resistant including Black Mesdag, Culberson (S.N. 295), Caucasus, Danish Island (S.N. 311) and Siberian (S.N. 323). A large number proved to be highly susceptible; the greatest number, however, could be placed in groups intermediate between the two extremes. Several varieties including Bicknell, Black Diamond, Danish, Danish Island, Early Gothland, Rossman and Scottish Chief appeared to manifest a greater susceptibility to Ustilago avenae than to Ustilago levis. The reverse seemed to be true in the case of C.I. No. 620, Green Russian, Monarch and Tobolsk.

All the varieties of Avena sativa orientalis appeared to be susceptible. The wild forms of Avena sterilis were moderately susceptible to both smuts. The cultivated varieties such as Burt, Fulghum, Red Rustproof and other varieties possessed a marked resistance to both smuts.

Gaines (11) tested 210 varieties and selections of oats for resistance to covered smut, Ustilago levis. In general the immune and resistant classes belong to the Burt and Red

Rustproof groups. The more resistant classes were usually of Kherson or Sixty Day type. The hulless and common groups were generally found to be susceptible, the outstanding exceptions being three Markton selections and four Red Rustproof x Black Tartarian hybrids which were immune.

Reed (34) was one of the first to observe physiologic specialization in both the loose and covered smuts of oats, Ustilago avenae and Ustilago levis, respectively. He inoculated oat varieties with smut from various sources and found that varieties resistant to smut from one source would be susceptible to smut from other sources. In a later publication, 1927, Reed (38) presented further evidence in favour of the existence of physiologic specialization in both smuts.

Wakabayashi (48) studied crosses of Red Rustproof, which is immune from covered smut, with Black Tartarian, which is susceptible. Immunity was dominant and it was concluded that several genetic factors were involved. Barney (2) in three different crosses suggested that reaction to loose smut could be explained upon a monohybrid, dihybrid and trihybrid basis, respectively. Reed and Stanton (37) in crosses between Fulghum, which is resistant to both loose and covered smuts, and Swedish Select, which is susceptible, presented evidence which indicated that resistance to both forms was dependent upon the same genetic factors. Both immunity and resistance were dominant over susceptibility. No case of linkage was observed. Gaines (11) studied the inheritance of Red Rustproof

in four crosses with susceptible varieties. In crosses with Black Tartarian and Abundance the results indicated that Red Rustproof carried three dominant factors for immunity, any one of which prevents the production of covered smut spores. In crosses with Large and Chinese Hulless, one factor apparently did not give complete dominance in hulless segregates, but otherwise the prepotency of the factors for immunity was similar in all four crosses. Reed (36) in a cross between a very susceptible A. nuda and a resistant A. sativa, Black Mesdag, obtained results which indicated that resistance to Ustilago avenae is dominant while susceptibility is recessive. The facts seemed to indicate that there was a single factor difference between the two parents. Hayes et al (18) in a cross between (White Russian x Minota) Minn. No. II-18-37 and Black Mesdag, state that there are separate factors which differentiate immunity and resistance. The results could be explained by two pairs of genetic factors, II and RR, for immunity and resistance, respectively, located in Black Mesdag. I might be considered to be epistatic to R. It was found impossible, however, to determine the exact genetic constitution.

Garber, Giddings and Hoover (14) studied the inheritance in a cross between Gopher, which is moderately susceptible to both loose and covered smuts, and Black Mesdag, which is immune. Their data was based on the F_3 and F_4 generations, and the results indicated that resistance to smut is an

inherited character with a single main factor difference, operating to determine resistance. In addition to this factor, however, there is at least one other that conditions the expression of the character. Transgressive segregation with respect to susceptibility occurred in the cross. Reed (39) studied the inheritance of smut reaction in crosses between varieties resistant and susceptible to both loose and covered smuts; between varieties resistant to covered smut and susceptible to both smuts; between varieties resistant to loose smut and susceptible to both smuts, and between varieties susceptible to both smuts. In a cross between Black Mesdag, which is resistant to both smuts, and Hulless, which is susceptible, the data in the F_2 and the F_3 suggests a single factor difference for resistance between the two varieties. The F_2 of a cross between susceptible Silvermine and resistant Black Mesdag gave similar results. A similar ratio was obtained when susceptible varieties were crossed with varieties resistant to loose smut, and when crossed with varieties resistant to covered smut. When two susceptible varieties were crossed all the segregates were as susceptible as the original parental varieties.

Inheritance of Colour.

Numerous investigators have studied the inheritance of grain colour in oats. Nilsson-Ehle (26) made a detailed study of this character in which he showed that there was a monogenic difference in some crosses between black and white, yellow and

white, and gray and white. Some crosses between black and white gave in F_2 a digenic ratio of 12 black : 3 gray : 1 white; black and yellow likewise gave a ratio of 12 black : 3 yellow : 1 white. In another cross between Gold Rain, a yellow variety, and Moss which is black, the F_2 consisted of four types; black, yellow, gray and white. Some crosses of gray with yellow gave in F_2; gray, yellow, yellowish gray and white. These results were explained on the assumption of three colour genes S for black, Gr for gray and G for yellow. In another black-white cross the F2 generation gave a segregation of 15 black : 1 white, indicating that the black colour is produced by two duplicate genes S_1 and S_2. In addition to these main genes, there were found several modifying ones, M_1, M_2, etc. which dilute the black colour. This explanation has been repeatedly confirmed by several investigators. Wilson (49), Gaines (10), Zinn and Surface (50), Garber and Quisenberry (15), Hayes, Griffee, Stevenson and Lunden (18) and Odland (28) found monogenic differences between black and white. Surface (45) and Love and Craig (21) in crosses between a yellow sativa and a black fatua obtained a segregation of 12 black : 3 gray : 1 white. Caporn (4) using three varieties of A. sativa in crosses with A. nuda observed the following ratios in F_2; gray x white = 3:1, black x gray = 3:1 or 15:1 and black : gray : white = 60:3:1.

Fraser (9) made a cross between Burt, which produces yellowish red grains, and Sixty Day which produces yellow grains. He obtained an intermediate colour in F_1 and in F_2 a

ratio of 48 red : 15 yellow : 1 white. The results were explained by supposing Burt to carry two colour genes, R for red and Y for yellow, and the Sixty Day variety one gene, Y^1 for yellow. Apparently R is epistatic to both Y and Y^1.

Materials and Methods.

Materials.

The parents, Monarch strain R.L.* 560, Heigira strain R.L. 559, Richland R.L. 172, Joanette strain R.L. 561, (Minota-White Russian) x Black Mesdag R.L. 374, Victory R.L. 159 and Banner R.L. 179 were obtained from various sources. Monarch strain, Heigira strain and Joanette strain are selections made by Bailey (1) from Monarch Selection (Etheridge), Heigira Rustproof C.I.* 1001 and Joanette C.I. 1880, respectively. The strain (Minota - White Russian) x Black Mesdag was obtained from Dr. H. K. Hayes at the University of Minnesota. Richland, Banner and Victory were obtained from Mr. L. H. Newman, Dominion Experimental Farm, Ottawa, Ontario.

The rust cultures were obtained at the Dominion Rust Research Laboratory, Winnipeg, Manitoba, from W. L. Gordon, pathologist in charge of oat stem rust investigations, and the smut cultures from I. L. Conners, formerly pathologist in charge of smut investigations at the same institution.

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* R.L. = Rust Laboratory number, C.I. = United States Cereal Investigation number.

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explained by supposing Bmmb to carry two colour genes, B
red and Y for yellow, and the ninth may variety one gene,
Y_1 for yellow. Apparently R is epistatic to both Y and Y_1

The varieties used as parents were selected on the basis of their resistance and yielding ability. A summary of the rust and smut reaction and yielding ability of the parents is presented in Table I.

Table I. Reaction of parental varieties to the seven physiologic forms of oat stem rust and to loose and covered smut, together with their yielding ability.

Parents	Physiologic Rust Forms								Smut		Yielding
	1	2	3	4	5	6	7	8	Loose	Covered	ability
Heigira strain	R	R	R	S	R	S	R		S	S	mediocre
Richland	R	R	R	S	R	S	R		S	S	mediocre
Monarch strain	R	R	R	S	R	S	R		S	S	mediocre
Joanette strain	R	S	R	R	X	S	S		S	S	mediocre
(Minota-White Russian)	SR	SR	S	S	SR	S	S		R	R	mediocre
x Black Mesdag											
Banner	S	S	S	S	S	S	S		S	S	high
Victory	S	S	S	S	S	S	S		S	S	high

R = resistant, SR = semi-resistant, S = susceptible and X = heterozygosity.

The data in Table I shows that the two most virulent forms are 4 and 6. To form 6 no varietal resistance has as yet been obtained, so consequently it was not included in the inheritance studies. Fortunately, under natural field conditions this form is not prevalent. With regard to the other forms there is sufficient varietal resistance to each form to build up synthetically resistance to all of them.

In the studies on the inheritance of rust resistance Richland, Heigira strain and Joanette strain were used as the resistant parents, while in the smut inheritance studies the strain (Minota - White Russian) x Black Mesdag was used. These varieties are comparatively low in yielding ability, so the high yielding varieties, Victory and Banner, were used in crosses with them. In Table II is a summary of the drosses made and the generations grown.

Table II. Crosses made and generations grown.

Crosses made	Generations Grown			
Heigira strain x Banner	F_1	F_2	F_3	F_4
Heigira strain x Joanette strain	F_1	F_2	F_3	
Joanette strain x (Minota-White Russian) x Black Mesdag				
Richland x (Minota-White Russian) x Black Mesdag	F_1	F_2	F_3	
Victory x (Minota-White Russian) x Black Mesdag	F_1	F_2	F_3	
Heigira strain x Monarch strain	F_1	F_2	F_3	

Methods.

The F_1 of these crosses was grown either in the greenhouse or in the field. When grown in the field these plants were sulphur dusted, so consequently no rust data was recorded in

the first generation. The F_2 and F_3 were grown in spaced five foot rows one foot apart with guard rows of Victory oats sown on both sides of each series. Homozygous resistant families were selected from the F_3 population and grown in a rod row test. From each of the families selected, two or three plant selections were made.

Studies of rust resistance were made both in the field and in the greenhouse. In the field an artificial rust epidemic was produced by inoculating plants of Victory oats in the greenhouse to all forms except 4 and 6. These plants were then transplanted to the field at intervals along the guard rows. Exceptionally high infections were obtained by this method. Inoculations in the greenhouse were made by hand with the use of an inoculating needle, excellent infections being obtained.

The smut studies were made in the field, only. The seeds were inoculated six weeks previous to planting by first thoroughly dusting them with spores. They were then moistened, with the hopes that the moisture would carry the spores into the crevices of the hull. It would have been preferable to dehull the seeds, but as the numbers were large this was not done.

The most extensive study, on the inheritance of rust reaction, was made with the cross Heigira strain x Banner. The F_1 was grown in the greenhouse during the winter of 1926-1927, and the F_2 was grown the following summer. A random

sample of 1000 plants was taken and the rust reaction of each plant recorded and the number of factors involved determined. These F_2 plants were inoculated with form 2 in the greenhouse and grown in the field during the summer of 1928. From the F_3, 87 homozygous rust resistant families were selected and placed in a rod row test during the summer of 1929. Each plot consisted of three rows and was replicated three times, the centre row only being harvested. As Heigira is resistant to forms 1, 2, 3 and 5, 100 susceptible and 100 resistant F_3 families were inoculated with forms 1, 3 and 5 to compare the inheritance of their mode of reaction with that of form 2, which was previously studied.

The Heigira strain x Joanette strain cross was made with the object of combining the resistance of these two varieties, in which it was hoped that strains resistant to forms 1, 2, 3, 4 and 5 would be produced. One hundred and thirty-six F_2 plants showing field resistance were inoculated in the greenhouse with form 4.

As the strain (Minota-White Russian) x Black Mesdag is resistant to both loose and covered smuts, it was crossed with Richland and Joanette strain in order to combine rust and smut resistance. So far rust data, only, has been obtained on these two crosses.

In the cross Victory x (Minota-White Russian x Black Mesdag) a study of smut inheritance was made. In this study 301 F_3 families were selected at random. Each family was

divided into two lots of 50 seeds each, one lot being inoculated with covered smut and the other with loose smut. These were planted in five foot rows, each plot consisting of two rows. The two parent varieties were similarly inoculated and sown side by side at ten plot intervals.

An experiment was planned to determine what effect smut infection had on rust development. Accordingly, three resistant varieties Richland, Heigira and White Russian were inoculated with covered smut and sown in the field. Twenty rows of each variety containing 25 seeds were sown and at five row intervals uninoculated seed was sown to serve as a check.

Studies on the inheritance of seed colour were made in all crosses in which the parents differed in this character.

Correlated studies were made between rust reaction and other plant characters, and between yield and such characters as maturity, heading, strength of straw and height.

Experimental Results.

The mode of inheritance of stem rust and smut reaction, the effect of smut on rust development and the inheritance of grain colour will be discussed together with a study of linkages or correlations between the various plant characters.

Inheritance of Reaction to Stem Rust.

Several crosses were studied both in the field and in the greenhouse, and in all cases resistance appeared to be dominant or partially so and governed by a single genetic factor. In one cross, Heigira strain x Banner, the inheritance of the mode of reaction to forms 1, 2, 3 and 5 was studied, while in another cross, Joanette strain x (Minota-White Russian x Black Mesdag) resistance to form 4 was studied. In all cases rust reaction was governed by a single factor. In the following discussion each cross will be treated separately.

Heigira strain x Banner. In this cross a study was made of the mode of inheritance in the F_2 and F_3 in the field and of the F_2 plants inoculated with form 2 in the greenhouse. The results are presented in Tables III, IV and V.

Table III. Segregation in F_2 for resistance and susceptibility to stem rust in the field in a cross between Heigira strain x Banner, and calculation of goodness of fit to a 3:1 ratio.

Rust Class	Observed	Calculated	Dev.	P.E.	Dev./P.E.
R	622	641.25	19.25	8.54	2.25
S	233	213.75			

The following symbols are used throughout: R = resistant, SR = semi-resistant, Seg. = segregating and S = susceptible.

The total observed numbers agree fairly well with the calculated indicating a good agreement to a single factor hypothesis as the deviation is less than three times the probable error.

Table IV. Breeding behavior of F_3 families for reaction to form 2 in a Heigira strain x Banner cross and calculation of goodness of fit to a 1:2:1 ratio.

Rust Class	Observed	Calculated	$o-c^2$	$\frac{o-c^2}{c}$
R	157	213	3136	14.7230
Seg.	502	426	5776	13.5587
S	193	213	400	1.8779
			x^2 =	30.1596

p = very small

The agreement is not very satisfactory, but when the resistant and segregating classes are combined the deviation is only 2.3 times its probable error, indicating that the departure from a 3:1 ratio is not particularly significant.

Table V. Breeding behavior of F_3 families for field rust reaction in a Heigira strain x Banner cross and calculation of goodness of fit to a 1:2:1 ratio.

Rust Class	Observed	Calculated	$o-c^2$	$\frac{o-c^2}{c}$
R	211	213.25	5.0625	.023740
Seg.	439	426.50	156.2500	.366354
S	203	213.25	105.0625	.492673
			x^2 =	.882767

P = high

The high value of P implies a rather good fit to a 1:2:1 ratio.

The data in Tables III, IV and V indicate quite conclusively that resistance in this cross is governed by a single genetic factor, and furthermore, as the same ratio exists in field as in the greenhouse, it indicates that the same factor is operative in both places and at all stages of maturity.

The following contingency, Tables VI, VII and VIII show the relation between field and greenhouse reaction.

Table VI. Relation between the F_2 field data and F_3 families inoculated with form 2 in the greenhouse in a Heigira strain x Banner cross.

		F_3 Greenhouse Reaction			
		R	Seg.	S	Total
F_2 Field Reaction	R	148	458	15	621
	S	9	44	178	231
		157	502	193	852

$c = .62 \pm 028$

The value of c is fairly high indicating a close agreement between field and greenhouse rust reaction.

Table VII. Relation between F_2 and F_3 field rust reaction in a Heigira strain x Banner cross.

		F_3 Field Reaction			
		R	Seg.	S	Total
F_2 Field Reaction	R	202	416	4	622
	S	9	23	199	231
		211	439	203	853

$c = .67 \pm .026$

The value of c in this case is also fairly high indicating a close agreement between F_2 and F_3 field rust reaction.

Table VIII. Relation between the rust reaction of F_3 families under field conditions and in the greenhouse inoculated with form 2 in a Heigira strain x Banner cross.

F_3 Field Reaction	F_3 Greenhouse Reaction: R	Seg.	S	Total
R	142	51	3	196
Seg.	13	404	2	419
S	2	17	176	195
	157	472	181	810

$c = .76 \pm .019$

The high value of c shows that there is a close relationship between field and greenhouse reaction. As a similar relationship exists between the rust reaction of F_2 plants in the field and in the greenhouse, it strongly indicates that in this cross there is a complete lack of mature plant type of resistance acting independently of seedling resistance. It would appear also that the factor which controls the reaction in the greenhouse is the same as the one that operates in the field. As the field epidemic was caused by several forms it suggests that the factor which governs the reaction to form 2 also governs the reaction to the other forms, 1, 3 and 5.

In order to definitely prove this hypothesis, 100 susceptible and 100 resistant F_3 families, of the Heigira strain

x Banner cross, were selected and inoculated separately with forms 1, 3 and 5. The data for this experiment are given in Table IX.

Table IX. The mode of reaction of F_3 families of a Heigira strain x Banner cross inoculated with forms 1, 2, 3 and 5 in the greenhouse.

	Greenhouse Reaction Forms				Field Reaction	
No. of F_3 families	1	2	3	5	1927	1928
100	S	S	S	S	S	S
97	R	R	R	R	R	R
1	R	R	R	S	R	R
3	SR:S	R	R	R	R	R

The susceptible families proved susceptible to all forms, while the resistant lines, with the exception of four, were resistant. One resistant family was susceptible to form 5, and three others inoculated with form 1 gave semi-resistant and susceptible segregates.

Heigira is apparently not pure for resistance as an occasional susceptible plant was observed. This fact may account for the susceptibility appearing in resistant lines. Then again such susceptibility may be due to mechanical mixture or to natural crossing. However, as so few families failed to breed true for resistance, the results show fairly conclusively that the reaction of these four forms is governed by the same genetic factor.

Heigira strain x Joanette strain. In this cross the object is to build up synthetically resistance to forms 1, 2, 3, 4 and 5. As has been previously stated Joanette strain is resistant to form 4 and Heigira strain to the other four forms. In 1928, field rust data were taken on a random sample of 1781 F_2 plants. Of this number, 1357 were resistant and 424 susceptible. On the basis of a 3:1 ratio the deviation from the theoretical was 21.25 ± 15.61, indicating a good agreement with a single factor hypothesis. The results are presented in Table X.

Table X. Segregation in F_2 for resistance and susceptibility to stem rust in the field in the cross Heigira strain x Joanette strain and calculation of goodness of fit to a 3:1 ratio.

Rust Class	Observed	Calculated	Dev.	P.E.	Dev./P.E.
R	1357	1335.75	21.25	15.61	1.39
S	424	445.25			

From the F_2 population, 136 resistant plants were selected and inoculated in the greenhouse with form 4. From this number 22 resistant, 63 segregating and 51 susceptible families were obtained. On the basis of a 9:7 ratio the deviation from the theoretical was 8.50 ± 3.90, indicating a good agreement with this hypothesis. The results are presented in Table XI.

Table XI. Breeding behavior of F_3 families for reaction to form 4 in a Heigira strain x Joanette strain cross and calculation of goodness of fit to a 9:7 ratio.

Rust Class	Observed	Calculated	Dev.	P.E.	Dev./P.E.
R	85	76.5	8.50	3.90	2.18
S	51	59.5			

The plants were inoculated the latter part of April, 1929, a month when the sunshine is quite strong. The growth was not vigorous, the plants being more or less unhealthy and weak. The infections were correspondingly poor and difficult to determine. However, even on more vigorous plants form 4 gives very inconsistent reactions. It appears that temperature is an important factor in determining the consistency or inconsistency of this form. W. L. Gordon, pathologist in charge of oat stem rust investigations at the Dominion Rust Research Laboratory, Winnipeg, in an unpublished report, states that temperature is an important factor in governing the reaction of form 4. At 50 to 60° F. this form gives constant reactions on Joanette strain; at 80° F. heavy infection and at intermediate temperatures, an X reaction.

In view of these facts, and as the numbers studied were small, no conclusions can safely be drawn regarding the number of factors controlling the reaction of form 4

in this cross. In spite of the poor rust infections, however, an important fact brought out by these results is that reaction to form 4 is inherited and that resistance to it can be transferred by hybridization.

Joanette strain x (Minota-White Russian x Black Mesdag). The object of this cross is to combine rust resistance to form 4 with resistance to both loose and covered smuts. No field rust reaction was recorded as neither of the parents show much resistance to the other forms. In order to study the inheritance of the mode of reaction of form 4 in this cross a random sample of 1000 F_2 plants was harvested and studied in the greenhouse. Two attempts were made to study the reaction of this form. The infections in the first trial were very poor so a second attempt was made in which the temperature was controlled as far as possible. In spite of this precaution inconsistent infections resulted. However, sufficient data was obtained on 225 families to demonstrate that resistance to form 4 is apparently governed by a single factor. The results are presented in Table XII.

Table XII. Breeding behavior of F_3 families for reaction to form 4 in a Joanette strain x (Minota-White Russian x Black Mesdag) cross and calculation of goodness of fit to a 1:2:1 ratio.

Rust Class	Observed	Calculated	$o-c^2$	$\frac{o-c^2}{c}$
R	75	56.25	351.5625	6.2500
Seg.	90	112.50	506.2500	4.5000
S	60	56.25	14.0625	.2500
			x^2 =	11.0000

P = .002

The low value of P indicates a very poor fit on the basis of a 1:2:1 ratio, but when the resistant and segregating classes are combined the deviation from the theoretical is 3.75 ± 4.38. Therefore, from the results obtained on the basis of a 3:1 ratio, it is safe to assume that a single factor governs the reaction to form 4 in this cross. Although the primary object of this cross was to combine rust and smut resistance, no smut studies have as yet been made. Those families resistant to form 4 will be tested for reaction to the two smuts.

Richland x (Minota-White Russian x Black Mesdag). Richland which is resistant to all forms except 4 and 6 was crossed with the strain (Minota-White Russian x Black Mesdag to combine rust and smut resistance. So far rust data, only, have been obtained. The F_2 and F_3 of this cross has been studied, and in both cases resistance was governed by a single factor. In Table XIII data are presented on 958 F_2 plants and in Table XIV on 176 F_3 families.

Table XIII. Segregation in F_2 for resistance and susceptibility to stem rust in the field in the cross Richland x (Minota-White Russian x Black Mesdag) and the calculation of the goodness of fit to a 1:2:1 ratio.

Rust Class	Observed	Calculated	$o-c^2$	$\frac{o-c^2}{c}$
R	251	239.50	132.25	.5522
SR	452	479.00	729.00	1.5219
S	255	239.50	240.25	1.0031
			x^2 =	3.0772

P = .22

The value of P is not particularly high, but when the resistant and semi-resistant classes are combined the fit to a 3:1 ratio is very good as the deviation is only 1.73 times the probable error.

Table XIV. Breeding behavior of F_3 families for field rust reaction in the cross (Richland x Minota-White Russian x Black Mesdag) and calculation of goodness of fit to a 1:2:1 ratio.

Rust Class	Observed	Calculated	$o-c^2$	$\frac{o-c^2}{c}$
R	53	44	81	1.8409
Seg.	82	88	36	.4091
S	41	44	9	.2045
			x^2 =	2.4545

P = .30

The value of P is indicative of a fairly good fit. When the resistant and segregating classes are combined the fit to a 3:1 ratio is very good as the deviation is 3 ± 3.87.

Relation Between Rust Reaction and Other Characters.

Heigira strain x Banner. The relationship between rust reaction, maturity and seed colour was determined in this cross. These determinations were made by arranging the two sets of data in the form of a two by three-fold contingency table. The data are presented in Tables XV, XVI and XVII.

Table XV. Relation between rust reaction and maturity of F_2 plants in a Heigira x Banner cross.

F_2 Rust Reaction	F_2 Maturity in Days. 46-51	52-53	54-55	56-57	58-59	60-63	
R	46	194	200	96	25	12	573
S	12	65	81	33	13	9	213
F_2	58	259	281	129	38	21	786

c = .086 ± .048

Table XVI. Relation between days to maturity and field rust reaction in F_3 families of a Heigirs strain x Banner cross.

F_3 Rust Reaction	F_3 Maturity in Days. 66.5	68.5	70.5	72.5	74.5	Total
R	8	14	12	8	1	43
Seg.	9	24	41	22	4	100
S	4	15	15	10	4	48
	21	53	68	40	9	191

c = ,22 ± .050

Table XVII. Relation between rust reaction and seed colour in F_3 families of a Heigira strain x Banner cross.

F_3 Rust Reaction.

F_3 Colour	R	Seg.	S	
White	18	41	20	79
Seg.	26	50	26	102
Yellow	4	10	1	15
	48	101	47	196

$c = .12 \pm .082$

The low value of c shows that there is no marked association between maturity and rust reaction or between rust reaction and seed colour.

Joanette strain x (Minota-White Russian x Black Mesdag). The relationship between seed colour and resistance to form 4 was studied in this cross. Joanette strain is black and (Minota-White Russian) x Black Mesdag is white. The data arepresented in Table XVIII.

Table XVIII. Relation between seed colour in F_2 and resistance of F_3 families to form 4 in a Joanette strain x (Minota-White Russian x Black Mesdag).

F_2 Seed Colour

Rust Reaction to Form 4	Black	Gray	White	
R	47	11	7	65
Seg.	71	6	4	81
S	44	5	4	53
	162	22	15	199

$c = .169 \pm .068$

The low value of c indicates quite conclusively that no relationship exists between seed colour and reaction to form 4.

Inheritance of Smut Reaction.

The inheritance of smut reaction has been studied in the cross Victory x (Minota-White Russian x Black Mesdag) strain. The former variety is susceptible to both loose and covered smut, while the latter is immune. The F_3 of this cross, only, was studied. In 1929, 301 F_2 plants were selected at random, 50 seeds of each being inoculated with loose smut and 50 with covered smut. Sufficient seed for checks of the two parent varieties was similarly treated. These were planted in five foot rows, each plot consisting of two rows of 25 seeds. At ten plot intervals the two parent varieties were sown. In recording the data the total number of plants in the plot and the total number showing smut infection were counted and the results expressed in percent.

The infections obtained, on the whole, were not high. Infections on the susceptible parent ranged from 4.4 to 23.8 percent for loose smut and from 2.2 to 28.9 for covered smut, while the resistant parent was completely immune. One hundred and eighteen of the F_3 families were immune to loose smut, 31 of which were more or less susceptible to covered smut. One hundred and twenty-six were

immune to covered smut, 39 of which were more or less susceptible to loose smut, while 87 families were immune to both. Twenty-two of the F_3 families inoculated with loose smut and 8 inoculated with covered smut were more susceptible than the susceptible parent, indicating that transgressive segregation had taken place. The distributions of parents and F_3 families for reaction to loose and covered smut are presented in Table XIX.

Table XIX. Distribution of the F_3 families and the two parent varieties for reaction to loose and covered smut.

Parents and F_3 Families	0.0 0.0	1.0 4.9	5.0 9.9	10.0 14.9	15.0 19.9	20.0 24.9	25.0 29.9	30.0 34.9	35.0 39.9	40.0 44.9	45.0 49.9	50.0 54.9	55.0 59.9
Loose Smut													
Parents:													
Victory	-	1	5	12	8	3	-	-	-	-	-	-	-
Minota-White Russian x Black Mesdag	29	-	-	-	-	-	-	-	-	-	-	-	-
F_3 Families	118	53	52	34	12	10	7	4	3	5	1	1	1
Covered Smut													
Parents:													
Victory	-	2	6	6	6	7	2	-	-	-	-	-	-
Minota-White Russian x Black Mesdag	29	-	-	-	-	-	-	-	-	-	-	-	-
F_3 Families	126	67	45	24	16	12	3	4	-	1	2	-	1

The data in this table apart from indicating that transgressive segregation has taken place, further suggest the possibility of a correlation between the infection capabilities of both loose and covered smuts. Accordingly the relationship between the percentage infection in both smuts was determined. A correlation coefficient of .519 ± .028 was obtained, a value which strongly suggests that such a relationship exists. The distributions are shown in Table XX.

Table XX. Distribution showing the relationship between the percentage infection in both loose and covered smuts in 301 F_3 families in a Victory x (Minota-White Russian x Black Mesdag) cross.

Percentages of Covered Smut	Percentages of Loose Smut													
	0.0	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.9	57.5	Total
0.0	87	14	18	4	3									126
2.5	17	21	19	8	1	1								67
7.5	8	12	8	10	4	1	1			1				45
12.5	6	4	3	6		3	1			1				24
17.5		2	3	4	2	2				2			1	16
22.5			1	1	1	1	3	3	1		1			12
27.5					1				1	1				3
32.5				1		1	1					1		4
37.5														
42.5						1								1
47.5								1	1					2
52.5														
57.5							1							1
Total	118	53	52	34	12	10	7	4	3	5	1	1	1	301

$r = .519 \pm .028$

Transgressive Segregation.

Twenty-two families inoculated with loose smut and 8 with covered smut, contained a distinctly greater percentage of smutted plants than did the susceptible parent. This indicates that transgressive segregation has taken place. It seems probable that the (Minota-White Russian) x Black Mesdag parent parent possesses one or more factors for susceptibility, and that the Victory parent has a factor which prevents complete susceptibility. On this assumption when the susceptible factor carried by the (Minota-White Russian) x Black Mesdag parent is associated with the susceptible factor of the Victory parent, increased susceptibility occurs. It is assumed that the (Minota-White Russian) x Black Mesdag parent is of the genetic constitution, RRss and the Victory parent rrSS and that the double recessive rrss causes increased susceptibility.

In order to determine, more completely, the mode of inheritance of smut reaction in this cross a detailed analysis of later generations will be undertaken.

The differentiation between resistant, segregating and susceptible classes is difficult with a character like reaction to smut which is not completely expressed in the progeny. However, resistant, semi-resistant and susceptible classes were formed by classing all families showing no smut infection as resistant, those showing more infection than the susceptible parent as susceptible and those showing infections

within the two extremes of the susceptible parent as semi-resistant.

By grouping the resistant and semi-resistant classes a very good fit was obtained on the basis of a 15:1 ratio in the families inoculated with loose smut, the deviation from the theoretical being 3.19 ± 2.83. On the other hand, the deviation from a 15:1 ratio in the families inoculated with covered smut was 10.81 ± 2.83, indicating a fairly wide departure from the theoretical. When the loose and covered smut classes are combined the deviation from a 15:1 ratio is 7.63 ± 4.01. The results are presented in Table XXI.

Table XXI. Breeding behavior of F_3 families for reaction to loose and covered smuts, and for both smuts combined in a Victory x (Minota-White Russian x Black Mesdag) cross and the calculation of goodness of fit to a 15:1 ratio.

Smut	Class	Observed	Calculated	Dev.	P.E.	Dev./P.E.
Loose Smut	R	279	282.1875	3.19	2.83	1.12
	S	22	18.8125			
Covered Smut	R	293	282.1875	10.81	2.83	3.81
	S	8	18.8125			
Loose and Covered Smut	R	572	564.3750	7.63	4.01	1.91
	S	30	37.6250			

The results obtained from this study, on the inheritance of smut reaction, prove that it is possible to obtain resistant strains from a cross between resistant and susceptible varieties. As only the F_3 of this cross has been studied it is difficult to suggest a genetical hypothesis to explain the results. However, it is evident that two factors at least govern smut reaction and that resistance is dominant.

Effect of Smut on Rust Development.

In this study two rust resistant varieties, Heigira strain and Richland, and one moderately resistant variety White Russian, were inoculated with covered smut. Twenty rows of each variety containing approximately 25 seeds were sown, and at five row intervals uninoculated seed was sown to serve as a check.

This project was not conducted on a very extensive scale, but the results obtained strongly indicate that smut infected plants are more heavily rusted than those non-infected. The results of this investigation are presented in Table XXII.

Table XXII. Showing the percentage rust infection on smut infected and smut free plants.

Treatment	Percentage Rust		
	Richland	Heigira strain	White Russian
Check	15.4	52.2	100
Smut free	11.5	56.5	100
Smutted	73.1	91.3	100

The White Russian variety, owing to the presence of an artificial rust epidemic in the field, was quite susceptible and no perceptible differences were observed in the amount of rust infection between smutted and non-smutted plants. However, the results obtained with the other two varieties, Richland and Heigira strain, show that rust infection is greater on smutted than on non-smutted plants. Richland showed a difference in rust infection percentage of 61.6 between smutted plants and plants inoculated but non-smutted and a difference of 57.7 between infected plants and the checks. A similar difference, though less marked, was obtained with Heigira. In this variety the difference in rust infection percentage between smutted and inoculated but non-smutted plants was 34.8 and between the smutted plants and the checks there was a difference of 39.1.

Although no differences could be observed in the amount of rust on smut infected and non-smut infected plants on White Russian it indicates that the presence of smut on a

	8.42	84.8
	6.66	86.5
	7.19	81.4

plant does not cause a decrease in the amount of rust infection.

Inheritance of Colour.

A study of colour inheritance was made in three different crosses. It should be pointed out, however, that the primary object of these crosses was to obtain resistance to rust and smut. Consequently the study of colour inheritance was considered as secondary in importance and was, therefore, not studied in detail in successive generations. No data were taken on the F_1 of these crosses. The F_2 was studied in all three crosses and the F_3 in one only. The three crosses will be treated separately in the following discussion.

Heigira strain x Banner. This cross is between yellow and white grained varieties, Heigira being the yellow parent. Data were taken on both the F_2 and F_3 generations. The F_2 data were taken on 91 F_2 plants only, as no greater number was available for study. From these F_2 plants 74 whites and 17 yellows were obtained. The deviation from a 3:1 ratio was 5.75 ± 2.79, indicating a fair agreement with a single factor hypothesis. The data are presented in Table XXIII.

Table XXIII. Segregation in F_2 for seed colour in a Heigira strain x Banner cross and the calculation of goodness of fit to a 3:1 ratio.

Colour	Observed	Calculated	Dev.	P.E.	Dev./P.E.
White	74	68.25	5.75	2.79	2.06
Yellow	17	22.75			

In the F_3, data were taken on 196 families. From this number 78 white, 103 segregating and 15 yellows were obtained. On the basis of a 7:8:1 ratio a P of .47 was obtained which indicates a good fit to this hypothesis. The data are presented in Table XXIV.

Table XXIV. Breeding behavior of F_3 families for seed colour in a Heigira strain x Banner cross and the calculation of goodness of fit to a 7:8:1 ratio.

Colour	Observed	Calculated	$(o-c)^2$	$\frac{o-c^2}{c}$
White	78	85.75	60.0625	.7004
White-Yellow	103	98.00	25.0000	.2551
Yellow	15	12.25	7.5625	.6174
			x^2	= 1.5729

P = .47

The goodness of fit was also calculated on the basis of a 15:1 and a 9:7 ratio and in both cases good agreements were obtained.

From the data in the above tables it appears that white is dominant over yellow. With regard to the number of factors concerned the F_2 and F_3 do not agree, but as the numbers in the F_2 are small no definite conclusions can be drawn from them. On the other hand, the results in the F_3 indicate quite strongly that two factors are operative.

Richland x (Minota-White Russian x Black Mesdag). This cross is also between yellow and white hulled varieties, Richland being the yellow parent. Data were taken on 535 F_2 plants and on 139 F_3 families. Of the F_2 plants, 320 were yellow and 215 white. On the basis of a 9:7 ratio the deviation from the theoretical was 19.06 $\pm$ 7.47, indicating that the departure from this hypothesis is not particularly significant. The ratio further suggests that yellow is dominant over white or partially so. The data are presented in Table XXV.

Table XXV. Segregation in F_2 for seed colour in a Richland x (Minota-White Russian x Black Mesdag) cross and the calculation of goodness of fit to a 9:7 ratio.

Colour	Observed	Calculated	Dev.	P.E.	Dev./P.E.
Yellow	320	300.9375	19.06	7.47	2.55
White	215	234.0625			

The results obtained from the F_3 families entirely disagree with those of the F_2 as a good fit was obtained on the basis of a 1:2:1 ratio. The data are presented in Table XXVI.

Table XXVI. Breeding behavior of F_3 families for seed colour in a Richland x (Minota-White Russian x Black Mesdag) cross and the calculation of goodness of fit to a 1:2:1 ratio.

Colour	Observed	Calculated	$o-c^2$	$\frac{o-c^2}{c}$
White	34	34.75	.5625	.01619
White-yellow	74	69.50	20.2500	.29137
Yellow	31	34.75	14.0625	.40468
			x^2 =	.71224

P = high

It is difficult with a character like grain colour to differentiate accurately between yellow and white. It is quite possible that a number of the F_2 plants are wrongly classified, as the breeding behavior in F_3 indicates that a single factor governs the inheritance of colour in this cross.

Joanette strain x (Minota-White Russian x Black Mesdag). The parents of this cross are black and white grained varieties, Joanette strain being black. In this cross the F_2 only has been studied. Data were taken on 884 plants selected at random, 672 of which were black, 160 gray and 52 white. On the basis of a 12:3:1 ratio a P of .78 was obtained indicating a close agreement to this hypothesis. According to this theory Joanette strain carries two dominant factors, B for black and G for gray, black being

epistatic to gray. The genetic constitution of the two parents is therefore BBGG and bbgg. Table XXVII contains the observed and calculated numbers from this cross.

Table XXVII. Segregation in F_2 for seed colour in a Joanette strain x (Minota-White Russian x Black Mesdag) cross and the calculation of goodness of fit to a 12:3:1 ratio.

Colour	Observed	Calculated	$o-c^2$	$\frac{o-c^2}{c}$
Black	672	663.00	81	.12
Gray	160	165.75	33.0625	.20
Yellow	52	55.25	10.5625	.19
			x^2 =	.51

P = .78

Heigira strain x Monarch strain. This cross is between yellow and black hulled varieties, Monarch strain being the black parent. Inheritance of colour in this cross was studied in the F_2 only. Data were taken on a random sample of 896 plants of which 670 were black, 128 white and 98 yellow. These numbers were fitted to a 12:3:1 ratio, but a very low value of P was obtained. The data are presented in Table XXVIII.

Table XXVIII. Segregation in F_2 for seed colour in a Heigira strain x Monarch strain cross and the calculation of goodness of fit to a 12:3:1 ratio.

Colour	Observed	Calculated	$o-c^2$	$\frac{o-c^2}{c}$
Black	670	672	4	.005952
White	128	168	1600	9.523810
Yellow	98	56	1764	31.500000
				$x^2 = 41.029762$

P = low

There are too many individuals in the yellow class, but as it is difficult to differentiate between yellow and white seeds the poor fit is considered to be due, largely, to errors in classification. But when the white and yellow classes are combined the deviation is 2 $\pm$ 8.74 indicating an almost perfect fit to a 3:1 ratio. However, as seeds definitely white and definitely yellow were observed, it is fairly safe to assume that two factors govern the inheritance of colour in this cross.

Yields on Rust Resistant Selections.

Yields have been obtained on rust resistant selections from the Heigira strain x Banner cross, only. From this cross 87 resistant families were selected in F_3 and grown in a rod row test together with 18 standard varieties.

	Observed	Calculated	$\sigma-\sigma_g$	$\frac{\sigma-\sigma_g}{\sigma}$
	670	675	4	.005952

These were grown at the Dominion Experimental Farm, Morden, Manitoba, during the summer of 1929, a year in which very little stem rust was present. No artificial rust epidemic was produced; consequently the yields obtained on these strains were not a test of their yielding ability under rust conditions. Under such conditions it would be expected that a number of these selections would outyield the more susceptible standard varieties. However, even under the conditions that did exist quite a number of the selections proved to be fairly high yielders, six of them showing higher yielding ability than Banner.

There was a considerable difference in the yields produced by the parents. Banner yielded 79.6 bushels and Heigira 64.8. The range in yield for the 87 strains was 83.8 to 40.6. Although these results are for one year only they indicate quite conclusively that it is possible by plant breeding methods to obtain high yielding rust resistant strains of oats.

Miscellaneous Correlations.

In the F_4 of the Heigira strain x Banner cross the degree of association between the following characters was studied.

Characters	Correlation Coefficient
Heading - Maturity	.735 ± .033
Heading - Strength of Straw	.304 ± .054
Heading - Height	-.089 ± .070
Height - Strength of Straw	-.135 ± .069
Maturity - Strength of Straw	.266 ± .027
Maturity - Height	-.186 ± .068
Yield - Maturity	.180 ± .068
Yield - Heading	-.077 ± .070
Yield - Strength of Straw	.054 ± .071
Yield - Height	.095 ± .070

The results show that a high degree of association existed between date of heading and date of maturity. Positive correlations, though less marked, were also found between heading and strength of straw and between maturity and strength of straw. Yield was not found to be associated with any of these characters.

Discussion.

The problem of breeding for resistance to stem rust and smut in oats has been studied by a number of investigators. Strains resistant to rust and resistant to smut have been produced, but none of them possess particularly high yielding ability. That is to say, when grown during a

season in which little disease is present these strains do not give as high yields as the ordinary high yielding commercial varieties. Therefore, from the practical standpoint, a great deal has yet to be accomplished.

The existence of physiologic specialization greatly complicates the problem. In Puccinia graminis avenae there are 8 known forms, seven of which have been found in Canada, the eighth in Australia, only. Therefore, in order to have complete resistance to stem rust, resistance to all forms must be obtained. At the present time this appears impossible as no varieties have as yet been found which are resistant to form 6. To all other forms, however, there is sufficient varietal resistance to build up synthetically resistance to them. Such resistance is sufficient for the present, as form 6 has been found only on rare occasions in Canada. However, there is no guarantee that this form or other such virulent ones will not become prevalent in the future. If this situation arises and no resistance in the meantime has been obtained to forms as virulent as 6, the production of resistant varieties will be an impossibility.

All investigators, with the exception of Dietz (6) in his studies with three genetically different strains of the Burt oat, agree that resistance to oat stem rust is dominant and governed by a single factor. No one, however, previous to the results presented in this thesis,

has studied the inheritance of the mode of reaction to physiologic forms in Puccinia graminis avenae. The results obtained show fairly conclusively that forms 1, 2, 3, 4 and 5 are governed by a single factor, and that forms 1, 2, 3 and 5 are controlled by the same factor, a fact which greatly simplifies the problem of breeding for stem rust resistance.

Physiologic specialization also exists within the smut fungi. Reed (38) made a fairly extensive study of physiologic specialization in smut by inoculating varieties with smut inoculum from various sources. This writer found that varieties resistant to smut from one source were susceptible to inoculum from other sources, and that some varieties were resistant to smut inoculum from all sources.

Studies of reaction to smut in oats have demonstrated that immunity, resistance and susceptibility are inherited characters and that strains resistant to both smuts can be produced. The results obtained in this investigation are in accordance with previous findings. As smut reaction is not completely expressed in the progeny, it is difficult to determine the nature and number of the factors involved in smut inheritance. However, in previous studies on the inheritance of smut reaction some investigators have assumed that a single factor hypothesis explained the results obtained, while others suggested two and three factor differences.

In the studies on the inheritance of smut reaction in a Victory x (Minota-White Russian x Black Mesdag) cross, there was evidence of transgressive segregation in families inoculated with loose and covered smuts. This result indicates that two factors at least govern the inheritance of smut reaction in this cross. No detailed genetic analysis has been made as one generation only has been studied. It is assumed, however, that the Victory x (Minota-White Russian x Black Mesdag) parent carries a factor for susceptibility as well as one for resistance and that the Victory parent carries a factor which prevents complete susceptibility. The genetic constitution of the two parents is therefore AAbb and aaBB respectively. Garber, Giddings and Hoover (14) also obtained transgressive segregation in a cross between Gopher which is semi-resistant and Black Mesdag which is resistant. These writers, however, used composite samples of smut inoculum and did not differentiate between loose and covered smut.

As a correlation coefficient of .519 $\pm$ .028 was obtained between the infection capabilities of loose and covered smut, it would suggest that both types of smut are similar in virulence.

It is the general opinion that the rust fungus thrives best on healthy plants. In an experiment to determine what effect smut infections had on rust development it was found that the presence of smut on a rust resistant variety

caused a decrease in its power of resistance. Weston (49a) obtained a similar result with wheat. This writer studied the effect of bunt infection of the host on the development of Puccinia glumarum Erikss. and Henn. and found that in general there was an increase in susceptibility of varieties to yellow rust when infected with bunt.

The studies on the inheritance of hull colour in a yellow - white cross, Heigira strain x Banner, the latter being the white parent, indicate that white is dominant to yellow. The F_2 data suggests that a single factor is operative, but as the number of individuals studied was small, 71, the results cannot be considered as indicative. The breeding behavior in F_3 indicates that two factors govern the inheritance of colour in this cross. In another yellow - white cross, Richland x (Minota-White Russian x Black Mesdag) in which Richland is the yellow parent, the F_2 data suggests that yellow is dominant to white and governed by two factors. The breeding behavior in F_3, however, indicates that there is a single factor difference between the two parents for colour of hull.

Nilsson-Ehle (26) in previous studies obtained monogenic differences between yellow and white hulled oat varieties, and according to Hayes and Garber (18a) results of crosses show that yellow is dominant over white or partially so.

In a cross between black and white varieties, Joanette strain x (Minota-White Russian x Black Mesdag), in which Joanette strain is the black parent, the segregation for

colour in the F_2 indicated a 12:3:1 ratio of black, gray and white. Joanette strain apparently carries two dominant factors, one for black and one for gray, black being epistatic to gray. In another cross between a yellow variety and Joanette strain, gray seeds also appeared, a result which substantiates the hypothesis that Joanette strain carries a factor for gray. A similar ratio was obtained by Nilsson-Ehle in a cross between black and white oat varieties. Ratios of 15 black : 1 white and 3 black : 1 white have also been obtained.

In a black - yellow cross, Monarch strain x Heigira strain, a ratio in F_2 of 12 black : 3 white : 1 yellow was obtained. Monarch strain is assumed to carry a factor for white as well as black. This ratio is not in agreement with results obtained by previous investigators. Nilsson-Ehle (26) in a cross between black and yellow varieties obtained a ratio of 12 black : 3 yellow : 1 white. In another yellow - black cross the same writer obtained in F_2, black, yellow, gray and white segregates. Surface (45) and Love and Craig (21) in crosses between a black fatua and yellow sativa obtained a digenic segregation of 12 black : 3 gray : 1 white.

The ultimate aim in rust and smut studies is to produce high yielding disease resistant varieties. Of the several crosses studied yields on rust resistant selections of the

Heigira x Banner cross only, were obtained. Eighty-seven F_3 resistant families were placed in a rod row test and of this number, under conditions in which no rust epidemic was present, six proved to have higher yielding ability than the Banner parent. Banner yielded 79.6 bushels per acre and Heigira 64.8. In a rust year it is to be expected that quite a number of these selections would give higher yields than the ordinary high yielding commercial sorts. These results indicate that it is possible to produce high yielding rust resistant varieties.

Summary.

1. The problem of breeding for complete resistance to oat stem rust, at the present time, appears impossible owing to the existence of form 6.

2. There is sufficient varietal resistance to all other known forms and resistance to them can be synthetically built up.

3. Rust reaction both in the field and in the greenhouse is governed by a single factor, and resistance in both cases is apparently dominant.

4. No relationship was found to exist between rust reaction and such characters as maturity and colour of glume.

5. The rust reaction of forms 1, 2, 3, 4 and 5 is governed by a single factor and forms 1, 2, 3 and 5 by the same factor.

6. It is possible, by breeding, to obtain high yielding rust resistant strains.

7. Oat strains immune to both types of smut can be produced without much difficulty.

8. Transgressive segregation took place in families inoculated with both loose and covered smut.

9. A fairly high correlation existed between the amount of infection in families inoculated with both loose and covered smut.

10. Smut infected plants are more subject to rust infection than non-smutted ones.

11. In two crosses between yellow and white grained varieties, digenic and monogenic differences were obtained. White is dominant to yellow in one cross and apparently recessive in the other.

12. In crosses between black and yellow and black and white grained varieties, black was dominant, and in both cases digenic differences were obtained.

13. A high correlation was obtained between date of heading and date of maturity. Positive correlations, though less marked, were also found between date of heading and strength of straw and between date of maturity and strength of straw.

14. Yield was not found to be associated with date of maturity and other characters.

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